Revue suisse Zool.	Tome 94	Fasc. 3	p. 545-551	Genève, septembre 1987

Spacial organisation during exploration and foraging in the harvester termite, *Trinervitermes Geminatus* [1]

by

M. RICKLI * and R. H. LEUTHOLD *

With 2 figures

ABSTRACT

When foraging parties of *Trinervitermes geminatus* leave their nests and subterranean galleries in search of food they lay pheromone trails. These trails have to be re-established at the beginning of every foraging excursion. Our paper describes the development of such foraging columns and the distribution of the termites on established trail networks. At existing forks in the trail traffic is often unequally distributed between the branches of the trail. If a termite arrives at a fork alone it tends to follow the more frequented of the two branches, but when walking in group formation termites often deviate to the other branch. When traffic is dense group formation is more frequent and at such times lone termites are more prone to deviation and once on the less frequented branch maintain their direction more persistently than when traffic is less dense. This explains the fact that minor trails are maintained during peak foraging activity and may be abandoned when activity decreases. The distribution of termites on a network is thus partially influenced by the level of general activity (social influence of the moment) and partially by the innate properties of the already established pheromone trail (influence of past social conditions).

* Division of Animal Physiology, Zoological Institute, University of Berne, Erlachstrasse 9*a*, CH-3012 Berne, Switzerland.

[1] Poster at the Annual Meeting of the Swiss Zoological Society in Berne, October 10/11, 1986.

INTRODUCTION

Termites of the West African species, *Trinervitermes geminatus,* leave their mounds through subterranean galleries in order to search for food, mainly dry grass. These tunnels lead into so-called foraging holes at ground level. From these foraging holes the termites continue their search for food sources above ground. At the hole they form columns and set out from the mound. The termites mark their trails as they go with trail pheromone, which is secreted from the abdominal sternal gland. Since *Trinervitermes geminatus* mainly forage at night and since the pheromone trail only remains active for less than a day, the foraging trail must be re-established at the beginning of each foraging excursion. The way the trail is remade is dealt with in the first part of this study.

This exploratory activity gives rise to a network of forked trails which spread out radially from the foraging hole in the opposite direction to the nest. It often occurs that the arms of a forked trail are not equally densely used. According to TSCHINKEL & CLOSE (1973), a trail which is more frequented has more pheromone than one which is used by few termites. In earlier laboratory experiments individual termites exposed to a fork in the trail where the two branches are unequally strong choose almost without fail the stronger branch of the fork. If termites behave in the same way in the field as in the laboratory the weaker branches of a pheromone trail network would predictably fade out rather quickly, and this can in fact be the case, although only when the total number of termites on the network is low (R. Leuthold, previous observation). Except in this situation we assumed that apart from the pheromone concentration on the branch there must be other processes steering the termite's choice of direction and thus the distribution of insects on the network. The second part of this study describes such processes. Several analyses of behavioural mechanisms have been carried out on harvester termites of the genus *Trinervitermes* (see HEWITT *et al.* 1969; TSCHINKEL & CLOSE 1973; OLOO & LEUTHOLD 1979; KAIB *et al.* 1982; LEUTHOLD & LÜSCHER 1984). The aim of this paper is to fill the gap with regard to a descriptive report of how trail systems are developed and thereafter selectively used by the termites under natural conditions.

MATERIALS AND METHODS

The observations described below were made at Lamto, a field station belonging to the University of Abidjan in the Ivory Coast.

All vegetation was cleared within a radius of 5 m of the *Trinervitermes geminatus* mounds which were to be studied. In this way it was possible to observe the termite columns without difficulty. For our observations we used a pair of binoculars (Wega Sport, 9 × 63) with specially adapted telefocussing (1.5-2.3 m) by way of a +2 diopter lens which could be mounted additionally. For nocturnal observation the field of view was illuminated by a strip light fixed parallel to the optical axis of the binoculars.

RESULTS

1. Laying the Network of Trails

Formation of the Termite Column: When the foraging hole has been opened the minor soldiers go out on to the ground and surround the hole (Fig. 1A); this circle of soldiers gradually spreads. Workers look out of the foraging hole but do not yet venture out (Fig. 1B). The circle of soldiers extends in one direction (Fig. 1C) and the workers then come out on to the ground (Fig. 1D). At this point the soldiers still form a boundary for the movements of the workers (Fig. 1E). As a column of workers gradually forms the soldiers' boundary breaks and workers start to go out into virgin territory where there are presumably no trails.

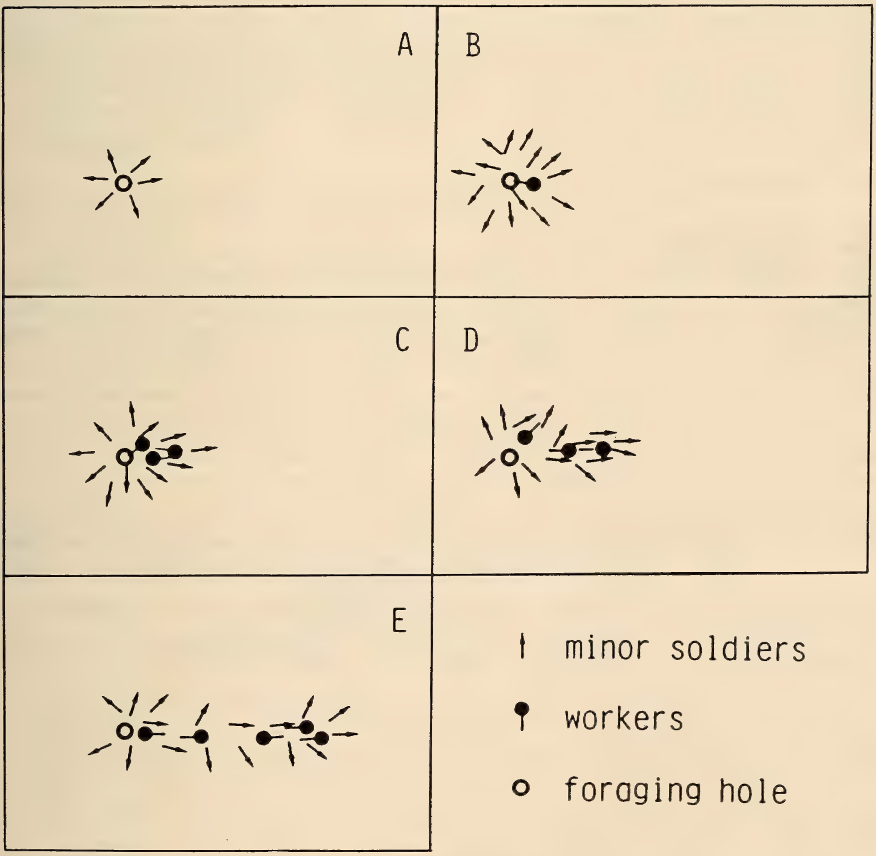

Figure 1.

Formation of the termite column setting out from the foraging hole (see text).

The Column's Choice of Direction from the Foraging Hole: Our observations of the formation of foraging columns revealed that a small number of leading individuals determined the direction the column takes. What are the criteria for this choice? Is it a continuation of the direction of the tunnel before it reaches the surface? We determined the direction chosen by 111 termite columns in relation to the mound (Fig. 2). Approximately twice as many columns set off in a direction at right angles to the mound-foraging hole axis as chose to continue this axis. Only one column endeavoured to march from the foraging hole to the mound. On the basis of these results we cannot draw any conclusions as to possible methods of orientation, although we deduce that the direction in which the column sets off is not chosen at random (Chi squared test, $p<0.01$).

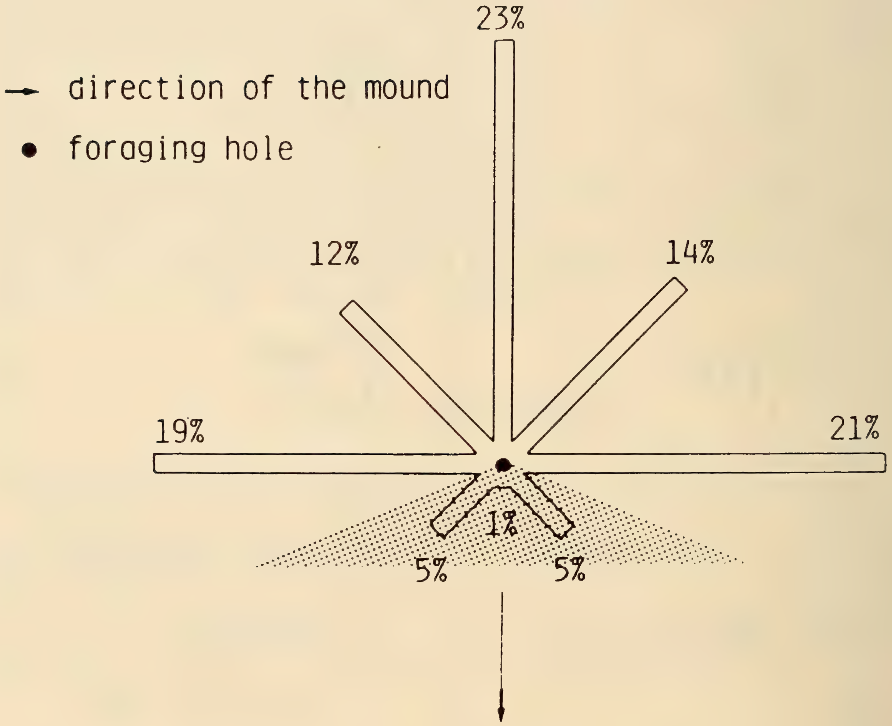

FIGURE 2.

Direction chosen by 111 exploratory columns in relation to the position of the mound. The shaded sector (135°) on the nest side of the foraging hole is significantly less frequented than the remaining sector (chi-squared test, p 0.01).

Spreading of the Columns: We repeatedly observed columns of termites which spread out in two different characteristic ways. One type consisted for the most part of individual insects (workers and soldiers) or small groups which advanced into virgin territory. It was concluded that the minor soldiers and workers laid pheromone on these exploratory excursions, since insects following later tended to choose the same paths and to turn back at the same points as the "pioneer" termites. In this type of column it is mainly the minor soldiers which act as pioneers. The second type of column, which formed when a great many termites left the foraging hole, was a continuous stream of insects which poured into virgin territory. The head of this column consisted of up to 95% workers. The first type of behaviour was more often observed than the second.

Forks in the Trail: According to our observations forks are made in the pheromone trail when it is first laid. It was observed that, in the case of a continuous stream of termites, numbers swell at the head of the column. Now and again a part of the mass broke away and went off to one side, thus forming a fork in the column. In the case of individual explorers or small groups at the head of the trail it seemed that forks were created especially at points where the pioneers stopped and the following insects turned back (analysed in the laboratory using a video recorder). It is possible that these points on the trail had a higher concentration of pheromone and thus induced some termites to break away from the main procession. At many forks the weaker trail was not used any more and subsequently faded out.

2. The choice of direction imposed on termites at trail forks

We observed that some trails in the network were used more intensively than others. According to the principle established by Tschinkel and Close (1973) concerning *T. trinervoides,* we suggest that tracks which, compared to others, are used more frequently right from the start have a higher concentration of pheromone and therefore attract a larger number of further termites, which then also add to the pheromone concentration. It has indeed been observed that individual termites which come alone upon a fork in the trail chose the statistically more frequented branch, a fact which implies that the trail *per se* exhibits a dominant attraction. However, since side trails are also used, despite their weaker attraction, in a natural context of social activity, there must be other factors which play a role in the choice of direction taken by the termite. We show below that, in addition to the characteristics of the trail itself, the behaviour of the rest of the community at the moment of choice can also influence that choice.

Termites are forced on to a weak side trail in dense traffic (Traffic density = number of active termites per time unit and distance unit): we observed that the termites' choice of direction at a fork shifted towards a less used branch when traffic became dense. On the other hand, with decreasing traffic less used branches could disappear. When traffic is dense 95-100% of all termites which are on that side of the column where the stronger trail branches off will take the stronger trail; termites on that side of the column where the weaker trail branches off will be more or less evenly distributed between both branches. When traffic is less dense, however, more termites walking on the side of the weaker branch tend to choose the stronger branch. We thus conclude that, when traffic is dense, a section of the column is forced on to the weaker branch at a fork.

Correlation between consistency of choice of direction and traffic density: We observed termites leaving the foraging hole individually and not joining a group, and noted whether they covered a complete 40 cm long test section or turned back midway.

At the same time we determined the number of termites leaving the hole per minute and were thus able to establish a scale for traffic density. Twenty-six observation series were made when traffic was light (up to approx. 20 insects per minute leaving the hole) and 25 when traffic was moderate (between 20 and 50 insects per minute leaving the hole). We observed that under the former conditions significantly fewer termites (average 61%, SD ± 21.5%) covered the whole test section than under the latter conditions (average 86%, SD ± 9%) (chi-squared test, $p<0.01$). We thus found that individual termites follow a pheromone trail for longer when traffic is more dense.

Consistency in following a trail among individual termites and groups: We observed that some termites in a foraging column move individually and others in integrated groups. These groups represent coherent units of two or more workers advancing one behind the other and keeping in close antennal contact. The groups were abundant when foraging activity was high and became rarer with decreasing activity. Groups advance faster than individuals and thus often overtake them. Groups are also more consistent in continuing their chosen direction than individual workers, which show a greater tendency to turn back, especially when the trail is weak. One typical example was that 80% of all individual workers walking on a unfrequented, weak, dead-end trail turned back within the first 10 cm and none at all went more than 20 cm along this track (total of 25 individuals observed), whereas a group of 6 termites turned back only after 50 cm and a group of 4 after 90 cm.

Behaviour of individual and group workers at forks in the trail: Individual workers approaching a fork were often seen to perform typical searching behaviour, i.e. they slowed down and, before choosing their way, intensively scanned the ground with their antennae. This was not the case among workers in a group. The whole group normally rushed by without showing such searching behaviour. The leading termite in the group appeared to be pushed by those following. Even though this behaviour could not exactly be quantified with the observation technique available, it was clear that termites integrated into groups chose minor side-trails more often than those moving individually.

DISCUSSION

Laying the Pheromone Trail

In the case of *T. geminatus* the minor soldiers play a decisive role at the outset of exploration in laying the network of foraging trails. It is these termites which are the first to leave the foraging hole and, by the direction they choose, they determine the direction the following columns will take.

This is evidence of an initial strict division of labour between the workers and the soldiers, which gradually decreases during exploration, as the workers also venture into virgin territory. The behaviour of *T. geminatus* minor soldiers thus falls between two known extremes. Among the related species, *T. bettonianus* and *T. trinervoides* minor soldiers do not take part in traillaying (Leuthold & Lüscher 1974; Hewitt *et al.* 1969; Tschinkel & Close 1973), whereas soldiers of the species *Nasutitermes costalis* make up the totality of explorers (Traniello 1981).

The Workers' Choice of Direction at a Fork in the Pheromone Trail

From the overall distribution of termites on a trail network it can be seen that the information provided by the pheromone is the dominant factor influencing the direction the termites choose at a fork. The pattern of the network of pheromone represents a tem-

porarily stable source of social information created by previous social behaviour. In addition, however, the density of traffic on the network has a definite influence on the use of minor side-trails. The density of traffic (activity of the colony) is a modulatory source of social information at that moment.

Thanks to the mechanisms described above individual termites spread over a certain area when activity is high in the colony and congregate on single pathways when activity is low. A different way of activating side-trails can be observed when termites move in groups. They usually continue to follow even very weak pheromone trails owing to their unhesitating progress. When the outdoor activity of the colony decreases, however, this mechanisms fails because the formation of groups becomes rarer. It is possible that the density of traffic is also an important factor in the exploration of the nest surroundings as in small colonies with few insects we never observed exploratory columns splitting.

We thus conclude that, when a large number of termites take part in foraging activities right from the start, several sources of food, i.e. tufts of grass, can be reached and exploited through one branched network of trails. If only few termites set out to search for food, as is the case in young colonies and large satiated colonies, the amount of food required is relatively small. In this case, it is sufficient if only one tuft of grass is used as a source of food since a complex network of trails would logically represent a loss of collective efficiency and defensive strength. Such a network is either not laid down from the start or else the weaker side-trails fade out when only few insects leave a colony towards the end of the foraging activity.

Acknowledgements

We are grateful to the Stiftung zur Förderung der wissenschaftlichen Forschung an der Universität Bern for their financial support of this study.

REFERENCES

Hewitt, P. H., J. J. C. Nel and S. Conradie. 1969. The role of chemicals in the harvester termites *Hodotermes mossambicus* (Hagen) and *Trinervitermes trinervoides* (Sjöstedt). *Insectes soc.* 16: 79-86.

Kaib, M., O. Bruinsma and R. H. Leuthold. 1982. Trail following in termites: evidence for a multicomponent system. *J. chem. Ecol.* 8: 1193-1205.

Leuthold, R. H. and M. Lüscher. 1974. An unusual polymorphism of the sternal gland and its trial pheromone production in the termite *Trinervitermes bettonianus. Insectes soc.* 21: 335-342.

Oloo, G. W. and R. H. Leuthold. 1979. The influence of food on trail-laying and recruitment behaviour in *Trinervitermes bettonianus* (Termitidae, Nasutitermitinae). *Entomologia exp. appl.* 26: 267-278.

Traniello, J. F. A. 1981. Enemy deterrence in the recruitment strategy of a termite: soldier-organized foraging in *Nasutitermes costalis. Proc. natn. Acad. Sci. USA* 73: 1976-1979.

Tschinkel, W. R. and P. G. Close. 1973. The trail-pheromone of the termite *Trinervitermes trinervoides. J. Insect Physiol.* 19: 707-721.